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FOREST INSECT INVESTIGATIONS

MELANOPHILA STUDIES OF THE 1936 SEASON AT THE HACKAMORE FIELD LABORATORY

Investigations into the biology and host relationships

by

A. S. West, Jr.
Berkeley, California
March 15, 1937

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MELANOPHILA STUDIES OF THE 1936 SEASON AT THE HACKAMORE FIELD LABORATORY

Investigations into the biology and host relationships

INTRODUCTION

Importance of Flatheads

Recognition of the importance of the role played by flathead borers of the genus Melanophila in the losses caused by insects in the eastside pine type in California has been given by Salman and Bongberg (1937). To properly interpret insect losses, attention must be given to all the factors involved. No one organism can rightly be construed to be the sole cause of the damage. Even where a single insect species is involved the effect of other factors such as climatic, physiographic and ecologic cannot be overlooked. In the case of beetle depredations in the forests of California where more than one species is concerned, proper evaluation of the role played by each species must be established. Heretofore little attention has been given to species other than Dendroctonus since the latter are the species present in the majority of cases where basal analyses of dying trees are made.

Stem analysis records show that in many cases where trees have apparently succumbed to an attack of the western pine beetle there was an earlier infestation of flatheads (Melanophila).

Incipient Stages of Flatheads

Such records have been based on the finding of galleries of full grown larvae in the bark of infested trees. The galleries of young larvae have been recognized in the past, but have not been considered in stem analysis work. In 1936, for the first time, attention has been given to the activities of these young stages which have been designated as incipients. A detailed discussion of incipients will be presented later. The results of their activities are evident in small winding ridges on the wood where developing broods are present. These ridges may be detected in long-dead trees. They have been produced by the healing over of the gallery as the young larva feeds. A reverse impression can be found in the phloem if the latter has not been consumed in subsequent brood development. Evidence of previous unsuccessful infestations by incipient stages frequently can be found imbedded in the wood.

Studies of the 1936 Season

During the 1936 season the work at the Hackamore Field Laboratory was chiefly devoted to a study of the biology and host relationships of flatheads. Biological studies were stressed since so little is known about the genus Melanophila. Some of the problems considered were: the species involved, its life cycle, the manner of feeding, effect of feeding upon the host, the host species, the effect of external factors such as climate upon the insect and the host, predisposition of host to attack, and flathead infestations in relation to attacks by other species.

1936 studies substantiated the fact that Melanophila californica is the species attacking standing trees. It is apparent that this species is more aggressive than M. gentilis in the insect complex of ponderosa pine. Californica was the only flathead species that emerged from a large amount of bark taken from standing infested ponderosa and Jeffrey pines. In the past there has been considerable confusion as to which species of Melanophila attacked green trees. M. gentilis was generally considered to be the more important species. However, Salman and Bongberg (1937) conclude:

"Gentilis appears to be the species chiefly concerned in infestations of felled trees and logs, windfalls, injured trees, and secondary bole infestations in standing trees.

Californica seems to be the species concerned in infestations in standing trees, although attacks by that species also sometimes seem to be of secondary importance."

Most of the bark used in emergence studies was collected from primary bole infestations so that the emergence of M. californica directly supports the conclusions of Salman and Bongberg.

LIFE CYCLE AND BIOLOGY

Previous Work

No great amount of work has been done on the life cycle of M. californica. Only brief notes are available in the literature or in the unpublished records of the Bureau of Entomology and Plant Quarantine. Such information as does exist has been summarized by Salman and Bongberg (1937). In connection with the studies reported in the following pages it is interesting to note that Burke (1919) believed that flathead borers of the genus Melanophila in general had one generation a year. He also stated, however, that some individuals of a particular brood might remain in the larval stage for several years.

Adult Emergence

Comparative Records

Emergence records for adults of M. californica are available for three years, 1934, 1935 and 1936. The data for the several years are not wholly comparable as noted below. In 1934 a small amount of bark was placed in rearing early in May. Emergence began on the 7th of that month, reached a peak on the 2nd of July, and ceased on the 2nd of August. In 1935, when emergence was recorded from the 17th of June, a peak was reached on the 17th of July, and the last adult was recorded on the 26th of August. In 1936, the collection of bark for emergence studies began early in June. Emergence, which was recorded from the 11th of June, reached a peak on the 22nd of June and ceased on the 3rd of August. In 1934 and 1936 all the material was collected on the Modoc National Forest. In 1935, a portion was from the Lassen National Forest. The 1934 figures include some emergence in cages on standing trees. In 1936, field observations showed that some emergence was already taking place during the first few days of June. The records of 1935 and 1936 are incomplete because of the late date at which the studies were started.

Temperature and Emergence:

Continuous temperature records secured at Hackamore make possible a comparison of emergence and temperatures. In Figures 1, 2, and 3, the daily emergence records are compared with the daily maximum temperatures of the three seasons. It is evident that the trend of emergence closely parallels the daily maxima. In each graph it will be noticed that the closest correlation was obtained during the period of greatest emergence. During the latter portion of the emergence period the correlation was frequently poor. The peak at the beginning of the 1936 record (fig. 3) does not necessarily indicate that the heaviest emergence was occurring at that time. A small lot of bark was in rearing at that time. A more representative record was secured when a larger amount of bark was in rearing. Since the amount of bark changed during the period of observation, emergence (fig. 3) is expressed as number of beetles per square foot. In Figures 1 and 2, the emergence is expressed as number of beetles.

Daily minima did not correlate with emergence in any but a most general fashion. Consequently means did not parallel emergence as closely as did maxima.

Emergence on Unit Basis:

An average emergence of 2.14 adults per square foot of bark surface was secured from the bark in rearing during the 1936 season. In the several samples of bark this figure varied from 0 to 8.1 individuals. However, these figures do not give the total emergence. In some cases not all the beetles emerging reached the collecting jars. It should be remembered that some emergence occurred before certain samples of bark were placed in rearing. With one exception the percent of adults not reaching the collection jars was small, and it seems likely that most of the bark was in rearing during the period of greatest emergence.

Field Observations:

Although emergence holes of M. californica were observed in the field early in June, no adults were seen. About the 23rd of August several adults were active in the vicinity of a couple of freshly felled trees. During July, one adult was attracted to the outside of a cage into which beetles were being introduced. Field notes of the 1934 season record adults of M. californica in flight during the latter half of June.

Furniss (1931), reporting a slash study near Hackamore, writes as follows:

"Melanophila californica Van Dyke was observed in the largest numbers. It was also the first to appear, one individual being taken on Log 3 June 21. The height of the oviposition period for this species occurred about the second week of July. On the 7th and 9th of July, numberous adults could be seen moving about in the crevices of the bark on the top and sides of the logs. They were also numerous on the piles of limbs. The sunniest exposures were frequented except during the hottest portion of the

day, when the top apparently became too hot and the beetles sought the cooler sides. Melanophila gentilis Lec., distinguishable by its purple iridescence, was not seen until the first of July; only three or four were seen and none was collected. This species seems to frequent the same places as M. californica."

Adult Life

Observation Conditions:

All observations on adult activity were made on caged beetles. Several types of cages were used, including: small laboratory cages; outdoor cages, 3 feet on a side; cages on the boles of standing trees; and cages enclosing entire trees, 15-25 feet in height. Frequent observations were made on the activities of the beetles introduced to the cages. In the case of the large tree cages it was possible for the observer to enter the cage and observe the beetles under what approached natural conditions. Flight was possible in these cages. In the other cages unfavorable conditions for flight or feeding probably accounted for the unsatisfactory results.

Tropisms:

Several lots of adults, up to 50 in number, were introduced into the small laboratory cages where activity was confined to crawling about on small pieces of bark. No direct response to light could be noted although the beetles were active during the day and became more quiescent at night. Uneven exposure of the cage to either artificial or natural light failed to elicit a phototrophic response. A definite thermotrophic response was indicaged. In the various types of cages the beetles became active during the morning hours when the temperature began to rise, and they became inactive during the late afternoon hours when the temperature began to fall. At night when beetles were brought within range of heat from a wood stove activity again was resumed, even though the beetles were not exposed to a direct light. The apparent thermotrophic response was expressed in the larger cages by considerable flight activity. During the warmer parts of the day the adults were disturbed easily and responded by flying about. During the cooler hours of the day disturbance usually caused the beetles to drop to the floor of the cage where they made no apparent effort to fly.

Feeding:

It was demonstrated conclusively that needle feeding is a necessary adjunct of adult life. When the beetles were confined on the bole of a tree or in the smaller cages where no needles were supplied, they became inactive and usually rested at the base of the cage. When needles were introduced, or were present as in the large tree cages, a considerable amount of feeding was evident. The needles were fed upon in the irregular manner that is characteristic of Buprestid species. All the needles of any one cluster were not necessarily injured. Usually the injured needles were chewed to such an extent that they broke or soon browned and died. So far as could be determined all the feeding occurred on the needles of the current season's growth. After a total of 217 beetles had been introduced to one of the tree cages the effect of feeding was

noticeable because of the numerous browned and broken needles. It is not improbable that, where a heavy flight of Melanophila occurs, some significant defoliation of the tree might result. This defoliation would, according to its intensity, have some effect upon the general vigor of the host.

Length of Adult Life:

Although it was impossible to determine with certainty the length of life of individual beetles, observations indicated that four days was the average under the various caged conditions. It is probable that the unsatisfactory conditions in some cages contributed to the shortness of life. In many cases the beetles were carried from the floor of the cages by ants. The longest length of life was recorded in one of the tree cages where the last introduction of beetles was made on the 21st day of July. One adult was alive and active in this cage on the 5th of August, indicating a life of at least 15 days.

Copulation and Oviposition:

No information was obtained during the season on either copulation or oviposition. Although the beetles were comparatively inactive during the night some feeding seems to have occurred. It is possible that copulation is a crepuscular activity and hence escaped observance. Although close observation was made when the beetles were active they seemed to make no attempt to oviposit.

Attempted Forced Attacks

Cages on Tree Boles:

On three large trees cages were erected on the bole in a manner similar to that employed in western pine beetle life history studies. The trees selected were sampled over a distance of 20 feet on the bole to determine that no current infestation existed. Cages were erected of copper screening. They covered 20-20 square feet of bole surface and were held about 5 inches away from the bole by the use of heavy wire braces. In the center of the screening a tobacco can cover was soldered. This afforded a convenient means for introducing the beetles. In each case the cage was placed on the south side of the tree in a location that received a goodly amount of sunlight. Unfortunately no feeding material was provided and apparently conditions for adult life were most unsatisfactory. Room for flight was exceedingly limited. In most cases the beetles fell to the bottom of the cage and showed but little inclination to crawl up the bole. The numbers of adults of M. californica introduced to the three cages were 89, 79, and 31. No activity was observed in these cages other than when the beetles were first introduced. Usually introductions were made late in the afternoon. Four days was the maximum length of life recorded in any of these three cages. A thorough examination of the caged areas will be made during the 1937 season to check the possibility that some infestation may have occurred. Judging from the shortness of life and the inactivity of the beetles it is extremely doubtful that an infestation became established.

Caged Trees:

To more nearly simulate natural conditions three small trees, ranging from 15 to 25 feet in height, were selected to be enclosed in cages. These trees were comparable in size to the heavily infested poles that were found in the Timber Mountain region near Hackamore. One (IV) was selected as an average tree as regards growth and general vigor. No past injuries were evident. The only abnormal condition was a fungous infection of the needles, possibly caused by Lophodermium pinastri (Ascomycetes, Hypodermataceae), a common obligate parasite of ponderosa pine in California. The cage had a base 9 feet on a side and was 12 feet high. An additional pyramid top to the cage exceeded the height of the tree by several feet. The framework was covered with galvanized screening and heavy cheesecloth. (See fig. 4).

Into this cage a total of 217 beetles were introduced during a period of 15 days (July 7-21), at the rate of from 1 to 37 per day. The first introductions were made by placing the beetles individually on a bole or on a branch. This method was not successful as the beetles frequently fell to the floor of the cage and failed to climb back up the tree. In spite of precautions some ants were present and would quickly carry off the beetles that fell to the ground. Subsequent introductions were made by placing the beetles on the tips of the branches where they could find some purchase among the needles. Many of the adults introduced in this fashion began feeding almost immediately and remained on the tree except during periods of flight. The amount of feeding already has been mentioned. Because of this extensive feeding activity and the seemingly natural behavior of the beetles it is believed probably that some infestation resulted from the introductions. A favorable indication was seen in the attraction of an adult of M. californica to the exterior of the cage while introductions were being made. In late October the covering of the cage was removed so that the tree will be exposed to natural conditions during the winter months. It is intended to recover the cage before the start of the 1937 flight season and introduce more adults. It is hoped these introductions will aid in securing information on adult habits. Another purpose of this experiment is to demonstrate the effect of M. californica on its host under known infestation conditions, particularly as concerns external manifestations of attack and intensity of infestation. It should also help in proving whether this insect species can kill healthy trees. Another point of information desired is as to the relative success of a series of attacks in successive season, since observations indicate that most flathead attacks consist of broods originating in more than one season.

Of the other two caged trees one (V, see fig. 5 &6) was selected as being of better than average growth and vigor. The other was selected as a poor specimen, somewhat stunted and supporting a heavy mistletoe (Phoradendron-skya) infection. Cages similar to the one described above were erected. 61 beetles were introduced to cage V during a period of 10 days at the rate of from one to 19 beetles per day. The feeding of even this small number of beetles had an evident effect on the tree. As in cage IV the feeding was well distributed over the tree, not being confined to any particular level or side. Cessation of emergence prevented introduction of adults to cage VI. It is planned to recage this tree during 1937 and force an attack after removing the mistletoe infection.

Forced Attacks on Logs:

In mid-June 3 logs were cut from an uninfested ponderosa pine (Keen's Class 3C). During the following 30 days 135 beetles were placed in the cage by 5 separate introductions. The first lot was almost immediately consumed by ants. The second lot showed but little activity, probably due to the fact that no feeding material had been provided. A few branches were placed in the cage before the remaining introductions were made. A considerable amount of needle feeding occurred, but there was no indication that the logs constituted any particular attraction. The logs were examined as follows: one in mid-August, one in mid-September, and one in late October. All the bark and phloem was removed from each log, but no evidence of attack was uncovered.

Egg Stage

No information was secured as to time or manner of egg deposition. According to DeLeon (1935) the eggs are laid in the bark crevices. After the eggs hatch the larvae bore through to the cambium. M. gentilis eggs are described as "flattish, roughly circular and light yellow in color", and are considered to have an incubation period of possibly two or three weeks. In tow or three specimens of the infested material that was examined the galleries of very small larvae were traced back through the phloem into the bark. No traces of the eggs were found.

Larval Studies

Larval studies were emphasized since it is the larval stage that causes the damage to the host trees. Studies were made on standing infested trees as well as on logs which were brought to the laboratory insectary. Samples were taken at regular intervals from 20 standing trees, and a total of 35 logs were under observation. In addition observations were made on felled trees left in the woods. In no case was the cycle of development completed into the pupal stage. Hence, all the studies are as yet incomplete and will be continued during the 1937 season.

All stage of larvae may be found in infested trees at practically any time of the year. Newly hatched larvae are of course found only during and immediately following the emergence period. More advanced larvae are present without regard to season. Prepupae may develop during the emergence period and yet not complete the life cycle during the then current season. Judging by these phenomena it would seem that larval development and consequently length of life cycle depends fully as much on host conditions as on external factors. It has been assumed previously that M. californica can complete its life cycle in one year. All the information secured during 1936 indicates that a longer cycle is more common.

Resume of Larval Feeding and Development:

Newly hatched larvae mine through the phloem to the region of the cambium where they mine in a general horizontal fashion. This feeding, which scores both wood and phloem, apparently may continue through several seasons. In contrast to this slow growth a period of rapid development occurs during the later larval life. The size of the feeding gallery is increased. Often

it is extended finger fashion before one direction is selected. The larva feeds diagonally outward through the phloem into the bark and makes a pupal cell usually within half an inch of the exterior. Here the larva ceases feeding and rests in the prepupal state. Observations of the 1936 season indicate that a considerable length of time may be spent in the prepupal state and that possibly there is an enforced diapause unrelated to temperature. Although no information has been secured on pupation apparently it occurs in the spring with the advent of warm temperatures. Transformation to the adult stage follows.

The time spent by the larva in the incipient stage can be determined accurately by tracing the course of the gallery in the wood. Where feeding has scored the wood surface subsequent healing forms a distinct scar (see fig. 7). The age of the gallery at any particular point can be calculated by the number of annual rings which have formed peripheral to the gallery. In several cases galleries were traced back three years. In June, 1936, many larvae were found which had long healed galleries behind them although the larvae were still in the small incipient state. There is little doubt that the larvae were at least a year old at that time. The feeding of the then current season could be determined easily since the healing of that portion of the gallery had just begun. During the summer the galleries were usually found to be healed to within half an inch of the point at which the larva was feeding. Healing does not continue beyond that point where the larvae begin to enlarge their galleries and feed outward into the phloem.

The finding of old galleries in the wood as well as the presence of dead larvae in current incipient infestations indicates a high mortality. A tree may be able to support successive populations of incipients over a period of years without succumbing to the infestation. The possibility remains that the feeding and healing may have some effect of which there is no direct manifestation in the host. This effect may be a factor in the eventual death of the tree. A separate study has been initiated to determine the nature of the tissues of the healing scars by microscopic examination. Stuch a study should shed some light on the possibility suggested above.

Types of Larval Development:

During the 1936 season three classes of larvae were differentiated. There were nately; those larvae originating as the current season's brood and remaining in the incipient stage; those larvae which had overwintered as incipients and continued in the same stage; and those larvae which developed from incipients to prepupal larvae in the course of the season. It is probable that some overwintering as large larvae not in the prepupal stage occurs. Prepupal larvae which have completed their development the previous season are not considered here.

Incipient Attacks: There is no evidence indicating that the initial attack is definitely selective, although it will be pointed out later that certain classes of trees are predisposed to attack. Galleries of newly hatched larvae are very small and line-like. The color of the larvae blends with the phloem and wood so well that the larvae are practically invisible. The first larvae of the 1936 brood were detected about July 1st. (see fig. 8). These very tiny larvae could be distinguished from

a second stage larva although no actual evidence of molting was uncovered. The mortality was high among all incipients. This fact is evident from the large number of galleries in which no larvae are found, from the number of actual dead larvae recorded, and from the number of galleries ending in pitch areas. (See fig. 9a,b). Larvae of the 1936 brood in standing trees and in logs cut late in the season remained in the incipient stage at the end of the season (November 1).

Second Year Larvae: Most of the brood in standing trees that were sampled consisted of larvae that were at least a year old. In some cases the galleries plainly indicated that the age of the larva was greater than one year. In the majority of cases where the gallery indicated a development of more than one year the larva had been unsuccessful. The development of incipient larvae continued in some of the trees without the larvae reaching the period of rapid growth by the end of the season.

Development from Incipient to Prepupal Stage: In a few standing trees and in most of the felled trees and logs the larvae reached the prepupal stage during the 1936 season. Many of the logs brought to the insectary had incipient stage larvae at the time they were cut. Several of the logs were cut when the larvae had already reached the rapidly growing stage. In all cases once the enlargement of the gallery had begun development was exceedingly rapid. Little mortality occurred after this point in the life cycle was reached. In Table I (page 10) data are given from three logs which were placed in rearing. No attempt has been made to reduce the data to a unit basis since only the time element is considered. In each case it is clear that the period of growth between incipient larval and prepupal stage was short.

Prepupal larvae appeared in the logs in rearing as early as the end of July, but in no case did they pupate. It is expected that these larvae will complete their development during the 1937 season. (Salman and Bongberg (1937), however, give a record of larvae of M. gentilis remaining two years in the transition from prepupae to adults.) This evidence makes it unlikely that the life cycle of M. californica is completed in one year, under conditions on the Modoc National Forest. The evidence at hand indicates that the larvae remain in the incipient stage for an indefinite period of time, that rapid growth and development of the prepupal stage is contingent upon the condition of the host, that time spent in the prepupal stage is the phenomenon of an enforced diapause rather than being a function of temperature, and that final pupation and emergence is dependent upon temperature. The above indications do not exclude the possibility that larvae of one brood, when feeding on a host that is succumbing to attacks of previous broods, might complete development in one year.

Tree Samples:

The attacks in the standing trees which were sampled varied from very light to very heavy. By continuing observations in subsequent seasons it is hoped to secure information on the effect of various intensities of attack and of different sequences of attack on the host trees. In those trees where the attack was light there was little development of the larvae during the season. As previously mentioned the mortality of incipient stages was

Number	Date of Sampling	Area sampled sq. in.	Total number larvae	Number Alive	Number Dead	Incipients Success-ful	Incipients Unsuccessful '35	Incipients Unsuccessful '36	Incipients Total	Assoc. with pitch blister or pitched out	Medium larvae	Large larvae in phloem-bark	Pre-pupae in bark
Log 13	6/13/36	39	16	8	8	8			8	8			
	6/20/36	22.5	3	2	1	2	7	1	8	1			
	7/1/36	30	1	1		1*	9	4	13	1			
	7/9/36	100	8	2	6	2	2	6	8	6			
	7/24/36	38	1	1		1*	2° +1		3	1			
	7/31/36	28	1	1			5					1	
	8/7/36	28					4						
	8/14/36	36	1	1								1-->	
	8/21/36	25										( )	
	8/21/36	24	3	3			1						2
Logs 25 -1- & -2- in alternate weeks	7/2/36	407	31	27	4	27	5	4	9				
	7/10/36	30	8	6	2	6	1	2	3				
	7/16/36	[redacted]	1 + (1)		1			1			(1)		
	7/24/36	16	4	4							<--4-->		
	7/31/36	16	(3)	(3)								(3)	
	8/7/36	16	4	4								4	
	8/14/36	16	2	2								2-->	
	8/21/36	16	2	2								1	1
	8/28/36	16	2	2									2
	9/4/36	22	1	1									1
Logs 25 -4- & -5- in alternate weeks	7/2/36	316	29	27	2	27	4	2	6	3			
	7/6/36	305	25	23	2	23	4	2	6	3			
	7/10/36	20	3	1	2	1	1	2	3	3			
	7/16/36	16	1 +(2)	1							1 +(2)		
	7/24/36	16	2	2							1	1	
	7/31/36	16	1 +(3)	1			1		1			1 +(3)	
	8/7/36	16	2	2								2	
	8/14/36	16	2	2								2-->	
	8/21/36	16	1	1									1
	8/28/36	16	1	1								1-->	

Legend: *Beginning to widen gallery °Older than 1935 ( ) galleries - larvae not found

TABLE I

Development of Larvae of Melanophila californica in Logs

high. (See fig. 9). In one tree there was an apparent 100 percent mortality in the bole area that was sampled. It is believed that this is a common phenomenon, for the number of unsuccessful incipient galleries in an infested tree always is high. Frequently there are indications of unsuccessful attacks extending back over a period of years. After the first of July larvae of the 1936 brood appeared in the samples from several trees. It is apparent that broods of at least two successive years of origin may be found in an infestation. As previously stated, indications are that incipients are not generally successful in a resistant tree for more than two seasons although continued attacks on such trees may occur. When the host does succumb, however, there may be larvae of at least two broods present. In one of the trees having a heavy attack of the 1935 brood which at the beginning of the season was in the incipient stage, numerous larvae of the 1936 brood were found during July and subsequent months. In this tree the percentage of unsuccessful incipients of the 1935 brood was high, possibly indicating that the tree was in a weakened condition. Toward the end of the 1936 season the larvae of the 1935 brood began to grow rapidly. This condition seemed to be confined to a strip on the southeast side of the tree. A few larvae had reached the prepupal stage before sampling was discontinued. The 1936 larvae did not develop beyond the incipient stage. This tree will be closely observed during the 1937 season to determine the pregress of the two broods.

Several specimens of Jeffrey pine were included in the samplings. In one tree a top-killing infestation had undoubtedly contributed to a weakened condition. Samples of the infected bole area revealed that a high mortality had occurred in the heavy brood of incipient flatheads. By the middle of July the larvae were beginning to enter the period of rapid growth. However, many of the growing larvae were being pitched out. In September prepupae were appearing but a high rate of mortality continued. In many of the samples the frass filled galleries were completely soaked with pitch and several large pitch blishers were found. This pitching may be a characteristic of flathead infested Jeffrey pines. A tree of this species felled earlier in the season had been severely attacked by flatheads over a large portion of the bole. Pitching had been so abundant that nearly all the larvae were pitched out before transforming to prepupae.

Log Samples:

Sample logs taken from infested trees were placed in rearing in a screened insectary (see fig. 10). These logs were paraffined on both ends to prevent too rapid drying. Logs so treated apparently furnished a suitable environment since in most logs where the brood was successful the larvae developed to the prepupal stage. In a few logs contamination by barkbeetles or roundhead borers obliterated the flathead infestation. Such logs were discarded. Logs from the felled trees were brought into the insectary at the time of felling. Other logs were brought in from the same trees later in the season. This allowed comparison to be made of logs which were left in the woods for a part of the season, and felled infested material left in the woods throughout the season. Table II (page 12) gives the results of sampling on this series of logs. Most rapid development occurred in the material left in

TABLE II

Development of Melanophila californica larvae in logs in insectary and woods

Sample	Date of Sampling	Area Sampled sq.in.	Total Number Larvae	Number Alive	Number Dead	Incipients Successful	Incipients Unsuccessful	Medium Larvae	Large Larvae	Prepupae	Remarks
36-11	7/10/36	24	4	4		4*	1				Felled 7/11/36
	7/17/36	15	6					6			and left in woods.
	7/24/36	48	3					1	3		
	7/31/36	16	4						4		* incipient of
	8/10/36	42	7	6	1			1	5		'36 origin.
	8/17/36	63	14	13	1				7	6	
	8/24/36	25	3	3						3	
	8/31/36	66	15	14	1					14	
FH-36 27 (10,11,14)	8/8/36	16	4	3	1				3		Felled 7/11/36
	8/14/36	28	4	4					4-->		Brought to insect-
	8/21/36	16	5	4	1				2	2	ary 8/8/36.
	8/28/36	16	2	2						2	
	9/4/36	22	5	5						5	
FH-36 27 (1, 2)	7/17/36	16	3		3		5				Felled 7/11/36
	7/24/36	16	7	5	2	5	2				Brought to insect-
	8/8/36	16	5		5	5					ary 7/11/36
	8/14/36	16	4	3	1			1	2		
	8/21/36	16	1	1			2		1		
	8/28/36	16	2	2					1	1	
	9/4/36	22	4	3	1				1	2	

the woods for the entire season. In this case large larvae appeared by the 24th of July and prepupae on 17th of August. In the logs which were left in the woods for a part of the season large larvae were first found on the 8th of August, when the logs were placed in the insectary, and prepupae were found on the 21st of August. In logs which were placed in the insectary on the 11th of July large larvae were not found until the 14th of August and prepupae until the 28th of August. The cause of this variation in development is probably temperature. The temperatures underneath the bark on logs lying exposed to the sun would be considerably higher than those under the bark of logs in the partially shaded insectary. It should be noted that the figures in Table II are not based on a uniform sample area.

Sampling Difficulties:

It has been found true in these investigations, as in similar studies on barkbeetles, that a great variation in brood intensity occurs in different samples. Because of the time consuming nature of the work it is usually impossible to secure a large enough series of samples from which a true average can be struck for any one date. In the case of standing trees it is necessary that natural conditions be disturbed as little as possible. Accordingly small sample areas are desirable on standing trees. In the case of logs in rearing the total area is so small that large samples are impossible.

Individual Rearings:

Several artificial methods of rearing individual larvae were tested, but no one method was entirely satisfactory. Indications are, however, that a satisfactory method can be evolved by the use of which larvae can be reared from the incipient to the prepupal stage. One method that was used consisted of placing a larva on a piece of phloem and bark and sealing the phloem surface with a piece of ordinary glass. Medium to large larvae reacted favorably under these conditions and in many cases began feeding immediately and continued their development in the bark. However, it was necessary to shave the bark down to the point at which the larva was feeding in order to observe the larva. Each observation disturbed the larva. Of a total of 80 active larvae on which this method was tried 25 were reared through to the prepupal stage. In a few cases the larvae were injured during examination while in other cases the larvae failed to continue feeding after being disturbed. Although the first prepupa was noted on the 27th of July no pupation occurred while the larvae were kept at the field laboratory at Hackamore. No changes have taken place since their removal on November 1 to Berkeley, although they have been exposed to room temperatures that should allow development. Of the 25 prepupae 14 still are alive (January 30). Of this number only two appear to be in good condition. Most of the mortality followed a gradual shrivelling of the larvae which probably was the result of unsatisfactory moisture conditions. Several larvae also were reared by sealing a piece of bark and phloem to the surface of the wood block from which it was originally removed.

Once larvae have reached the prepupal stage they need no longer be disturbed and can be observed through the glass cover. Under natural

conditions, however, the prepupal larva is embedded in a bark cell so that exposure to light is a definite departure from normal.

For the rearing of small, incipient larvae a piece of phloem was sealed between two pieces of glass. The chief difficulty in using this method is that of obtaining the proper pressure on the larva. If the phloem does not fit snugly against the glass the larvae apparently cannot feed. Too great a pressure prevents the larva from moving at all. The best results were obtained when the larva was left in the gallery in which it had been feeding, and the phloem used was that in which the larva was found. Proper moisture conditions and the prevention of contamination are requisite. It was found that if the individual rearings were placed in a can having a tight fitting cover and containing a small moistening pad the phloem did not dry out. Although sterilization of the glass plates was adopted as sanitary measure fungous contamination was not eliminated. If the larva starts to feed at all it can be left for as long a period as a month without changing the phloem. This of course applies to small larvae in the incipient stage. When the larva reaches the period of rapid growth it will consume the phloem in a short period of time. 20 rearings of this type were brought to Berkeley on the first of November. Of this number only one has been successfully continued in rearing to date (2/4/37). This one larva was placed in rearing on the 24th of September and has grown from the small, incipient stage nearly to the prepupal stage. It is believed that by changing the food supply at intervals it will be possible to rear individual larvae successfully in this manner.

HOST RELATIONSHIPS

Susceptibility

Melanophila californica infestations are common throughout the east-side ponderosa and Jeffrey pine type. The discovery of incipient stages in green trees shows that this insect is more generally distributed than was previously supposed. On the Modoc forest the infestations are heavier in stands growing on poorer sites and along the timber margins. Some heavy infestations have been found on the better sites. Sufficient data have not yet been collected to determine accurately the relative susceptibility of the various tree classes to flathead attack. During the 1936 season several lots of analyses were taken on the Lassen and Modoc forests. In all cases the number of trees was small. These small samples cannot be used for any predictions, but there is an indication that the degree of susceptibility to flathead attack is in at least partial agreement with both Keen's and Dunning's susceptibility range.

Plot Studies

To obtain more information on the relative susceptibility of tree classes to flathead infestation, 6 plots of 2½ acres each have been established. It is expected that the plot studies will be continued over a period of years. Two of the plots are on Modoc survey plot MC-2 (Site III) and four on MC-3 (Site IV). Each living tree over 12" D.B.H. has been tagged, spotting data have been recorded, and a basal analysis has been made. A total of 89 trees were tagged on the MC-2 plots. No incipient infestations were found in basal analysis. However, 7.8% of the trees were definitely estimated to be

infested and 11.2% of the trees were noted as possibly being infested. On the MC-3 plots a total of 57 trees were tagged and examined. Incipients were found in the basal analyses of two trees. 10.6% of the trees were definitely estimated to be infested and 8.8% possibly so. The reasons for estimating the presence of incipient infestations where no incipients were found in basal analyses are based on the findings of Salman and Bongberg (1937). These authors showed that the bulk of flathead infestations were confined to the upper two-thirds of the boles of trees. Basal analysis, particularly by a small sample, would not indicate all the trees which are actually infested. These estimates were not based on any concrete factors. They were the result of the spotter's judgment gained from the examination of trees known to be infested with flathead incipients. It is hoped that by a large series of analyses of trees infested with flathead incipients it may be possible to build up definite criteria for the determination of infested trees which cannot be analyzed.

During the 1936 season a survey was made of the Timber Mountain plot of 40 acres. Half of this plot has been logged selectively. All trees were sampled for incipient flathead infestation. Where incipients were not found estimates were made as to the likelihood of their presence. The information obtained from this survey is summarized in Table III (page 16).

This plot which is located on the fringe of timber type demonstrated the abundance of incipient infestations in green trees growing on poor sites. Approximately 75 percent of the trees either were found to be infested by incipients or were suspected of being infested. The intensity of infestation varied from very light to very heavy. In all trees in which successful incipients were found examples of unsuccessful incipients attack also could be demonstrated. Frequently there were indications that the attack had continued over a period of years.

Another set of analyses was taken in the vicinity of Eagle Lake on the Lassen forest where the stand was composed of ponderosa pine, incense cedar and white fir. 42 percent of the trees had incipient flathead infestations. The figure would have been 9.5 percent if the examinations had been limited to basal analysis. On the Shaw cutover on the Modoc forest 66.7 percent of the trees were infested. 38.2 percent of the trees would have been recorded as infested if the examinations had been limited to basal analysis. These figures indicate that the estimates of percent of infested trees on the Timber Mountain plot (73.7 and 75.7 percent respectively for the cut and uncut areas) may be more nearly correct than the figures of 57.6 and 46.1 percent which resulted from basal analysis alone.

Host Species

During the 1936 season the survey crew analyzed green trees that had been felled on the Fruit Growers logging operation on the Lassen National Forest. Attention was paid to incipient flathead infestations in particular. Some of this data was secured in mixed stands of ponderosa and Jeffrey pine. Although the basis was small there is a strong indication that in such mixed stands flatheads show a preference for Jeffrey pine. The following figures were obtained in four random samples and a one-chain strip survey in the vicinity of the Harvey Ranger Station. (Table IV, page 16).

TABLE III

Flathead Infestation on Timber Mountain Plots

	Cut			Uncut		
	Trees	%		Trees	%	
Green trees	99			152		
Trees killed (1934-6)	40	28.8		84	35.6	
Trees at start (1934)	139			236		
Trees killed						
Felled trees	6			1		
Flathead in infestation	10	25.0		18	21.4	
Incipients present	9	22.5		36	42.9	
No flatheads or incipients	15	37.5		29	34.5	
Green trees						
Incipients found successful	44	44.0)	57.6)	44	28.9)	46.1)
Unsuccessful	13	13.1)	)	26	17.1)	)
Incipients suspected	16	16.2	73.7)	45	29.6	75.7)
Incipients not found or suspected	26	26.3		37	24.3	

TABLE IV

Percent of Ponderosa and Jeffrey Pines with Incipient Flathead Infestations

HOST		
Ponderosa Pine	Jeffrey Pine	Both Species
33.3	62.5	50.0
0.0		
28.6	61.5	47.6
8.0		
12.5	23.1	17.6

The relative importance of the role played by flathead borers has been established. Recognition has been made of the incipient stages of larval development. The adult emergence period extends from the middle of May into August with the greater portion occurring within a short period in June or July. Adult emergence correlates directly with maximum temperatures. Average adult life under caged experimental conditions was 4 days, with one record of 15 days. Activity of adults indicates a positive thermotropic response.

Intensive studies of flathead infestations in the Lassen and Modoc forests have shown that flatheads were concerned in the infestation of 50.1 percent of the ponderosa pines and 76.7 percent of the Jeffrey pines killed by insects. Flathead infestations were composed of successful and unsuccessful attacks. Recognition has been made of the incipient stages of larval development rather than of incipients. It has been suggested that the greater abundance of flatheads in Jeffrey pine might be correlated with the development of the Jeffrey pine beetle, Dendroctonus jeffreyi. This species has but one generation a year. Greater flathead infestations for ponderosa pine might be the result of more intense infestation by the western pine beetle, Dendroctonus brevicomis which has two generations a year. However, the fact that the differences in flathead infestations correlate directly with maximum temperatures on the basis of incipients in green trees and of successful flathead broods in infested trees is of the average ponderosa pine as to be definite preference as Jeffrey pine as host with this record does not easily detract from the theory that competition with species of Dendroctonus is a part of the explanation. In the analysis of killed trees by flathead infestation, 56.5 percent of the ponderosa pines had bole infestations and 78.1 percent of the Jeffrey pines were infested in the bole region. The bole of the tree is the region where the flatheads are in competition with the species of Dendroctonus and the difference in the life cycle of the two species may well account for this situation. It must be remembered, however, that the evidence at hand indicates that the life cycle of M. californica takes longer than one year to complete. Thus attacks resulting in advanced brood stages of flatheads in mixed infestations must have taken place previous to the time of attack by barkbeetles.

It is probable that with the accumulation of more data some correlation can be established between the abundance of flathead incipients and the stand factors of site, composition and type. At present the indications are that the incipients are more abundant on the poorer sites and that in mixed stands Jeffrey pine is more susceptible to attack than ponderosa pine. The abundance of flathead incipients is in itself an indication of the primarity of flatheads and their importance in insect losses.

SUMMARY

The importance of the role played by flathead borers has been established.

Recognition has been made of the incipient stages of larval development.

The adult emergence period extends from the middle of May into August with the greater portion occurring within a short period in June or July.

Adult emergence correlates directly with maximum temperatures.

Average adult life under caged experimental conditions was 4 days, with one record of 15 days.

Activity of adults indicates a positive thermotropic response.

Needle feeding is a requisite of adult life.

Attempted forced attacks on boles of trees were apparently unsuccessful

Attempted forced attacks on logs were definitely unsuccessful.

Attempted forced attacks on entirely caged young trees gave some promise of success.

Practically all stages of larval development can be found at any time of the year.

The life cycle of Melanophila californica in northern California is generally longer than one year.

Indications are that the length of life cycle depends fully as much on host conditions as on external factors.

The length of time spent in the incipient larval stages depends on the condition of the host.

The growth from incipient to prepupal stage is very rapid.

The duration of the prepupal stage is apparently dependent on an enforced diapause.

The feeding of the incipient stage larvae injures both wood and phloem.

The gallery made by the larva is healed over by the cambium.

The age of the healed gallery in the wood at any point can be determined by the number of annual rings peripheral to the gallery.

A small amount of data indicates that the susceptibility of ponderosa pine to flathead attack partially agrees with the susceptibility ratings of Keen and Dunning.

Incipient flathead infestations are widespread in northern California.

Many trees bear evidence of continued unsuccessful incipient attacks.

In mixed stands of ponderosa and Jeffrey pine the latter is apparently the preferred host.

CONCLUDING REMARKS

During epidemic western pine beetle infestations the part played by flathead beetles is overshadowed to a large extent, although it is none the less important. This is due to the fact that incipient galleries are concealed by the work of Dendroctonus and other species. Apparently the flathead incipients do not farewell in competition with the rapidly developing pine beetle larvae. It may be that for this reason flathead trees, as indicated by basal analysis are difficult to locate while the losses caused by Dendroctonus are high. When these losses fall off, as during 1936, the work of flatheads, particularly in the incipient stages, becomes more evident.

The establishment of definite factors by which trees containing flathead incipients can be recognized is a project on which work already has been undertaken. Whether or not this can be accomplished will depend upon the relationship of insect and host. It is not as yet known whether continual attack by flatheads produces a weakened tree or if the tree is weakened by other causes such as drought and hence is attractive to the flatheads. It is possible that both conditions may occur. Since complete analyses are necessary if detailed information on flathead infestations is to be secured, the study of host relationships can best be made by following loggers on a timber operation. In such an investigation numerous factors should be considered. Some of the factors are: bark thickness, length of needles, needle complement, rate of growth, age, class, site, exposure, soil, and presence of other insect species such as Chionaspis and Matsucoccus.

Some progress has been made in the biological studies that were inaugurated in 1936, but this work must be continued to fill the many lacunae existing in our present knowledge. Study of the feeding habits of incipients and of the physiological effects of the scars of healed galleries on the tree is of primary importance. As a mechanical factor the importance of these healed galleries may be negligible, but as a physiological factor their presence warrants further consideration.

Continued investigation on the basis set up in 1936 should establish more definitely the role of flatheads in the losses caused by insects.

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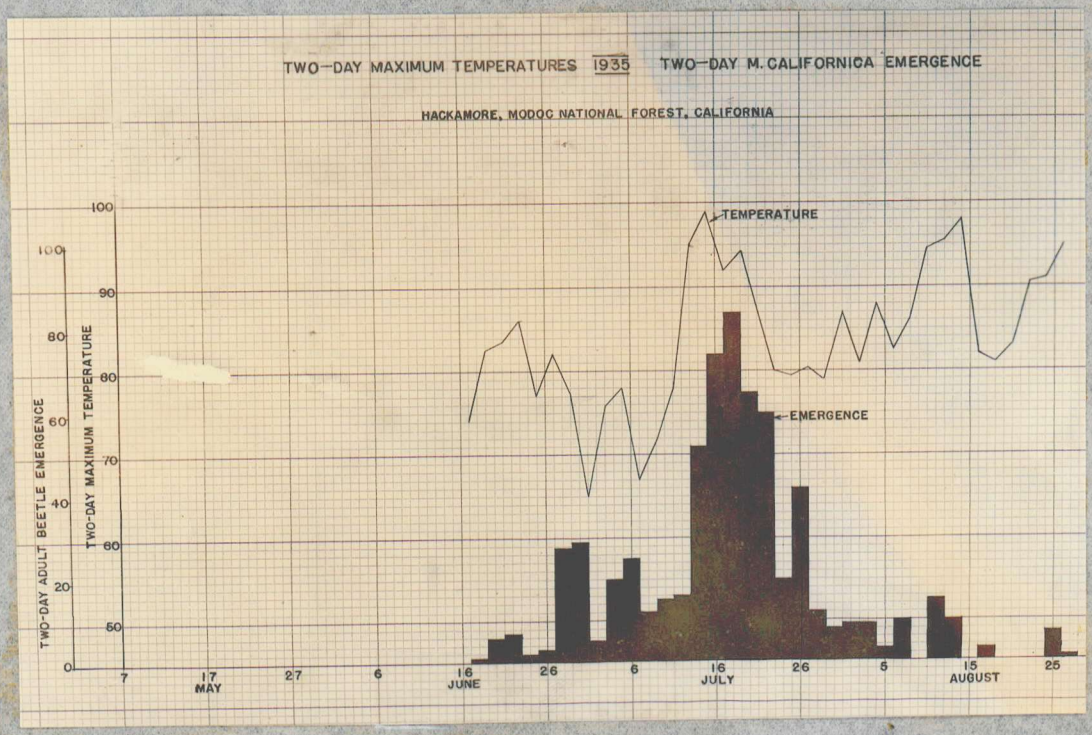
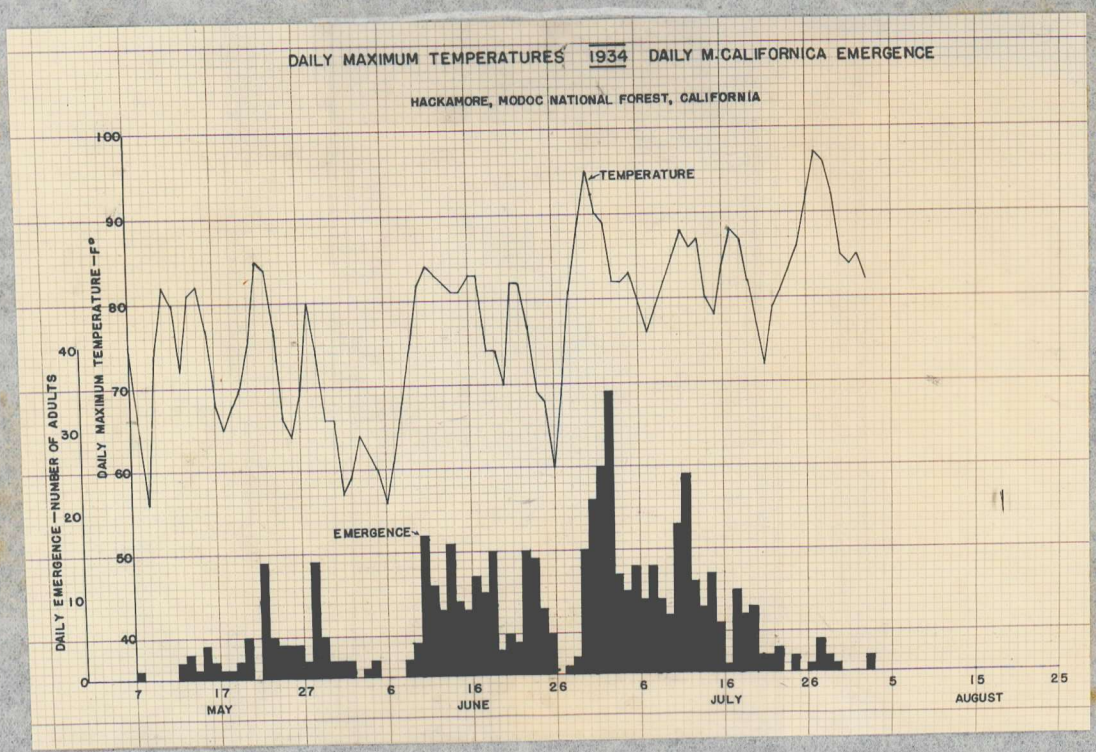


Figure 1

Emergence of Melanophila californica compared with daily maximum temperatures. 1934



Emergence of Melanophila californica compared with daily maximum temperatures. 1935

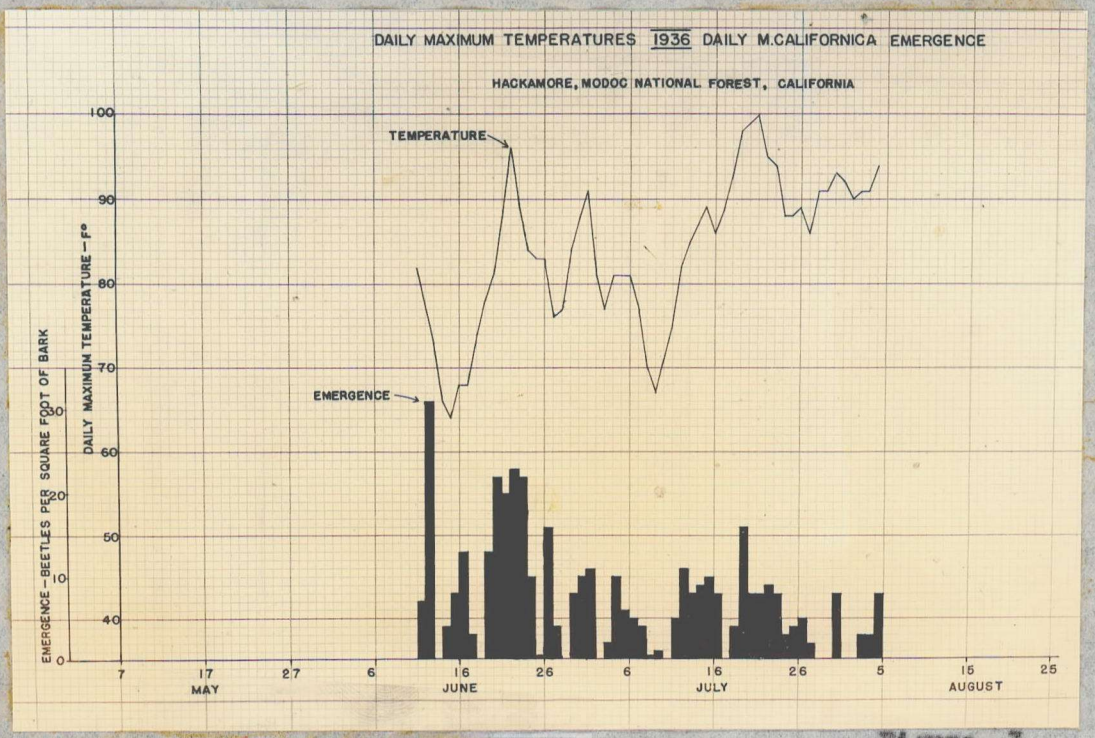


Figure 3
(above)

Emergence of Melanophila californica compared with daily maximum temperatures. 1936

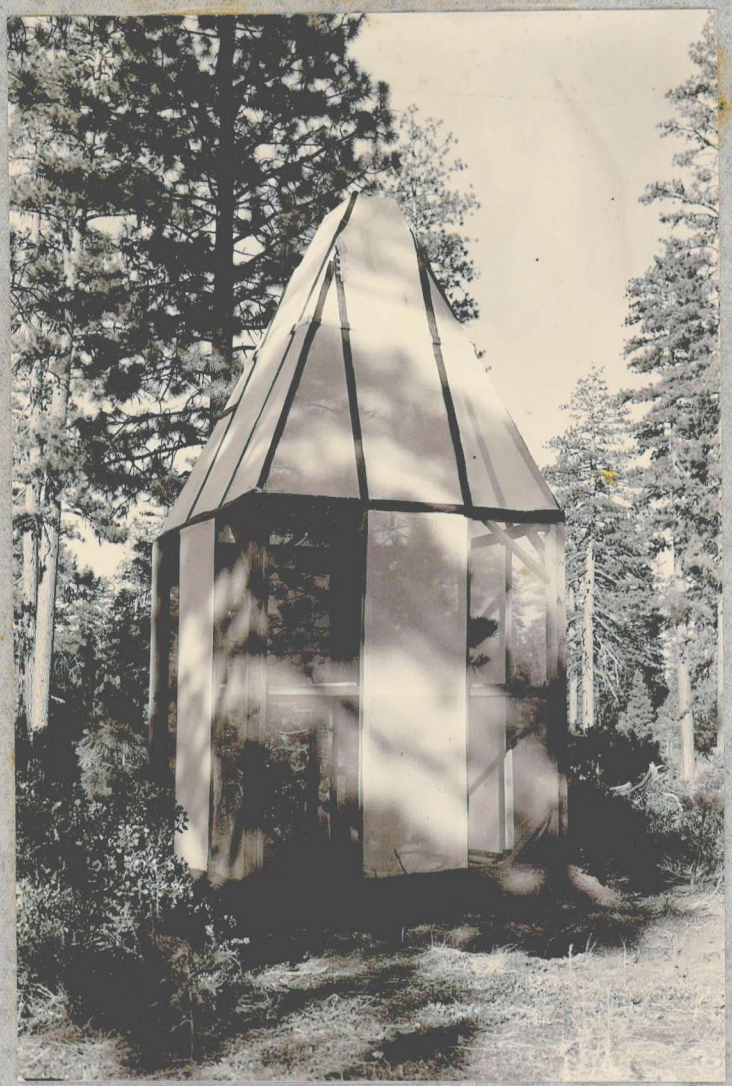


Figure 4
(left)

Tree cage IV enclosing ponderosa pine pole of average vigor. Photo by KAS. (9745B)

Figure 5

Cage V in process of construction. Photo by KAS (9745A)

Figure 6

Poorly growing ponderosa pine selected for Cage VI. Photo by KAS (9745)

FIGURE 7

Surface of sapwood of a specimen of ponderosa pine showing healed over scar of flathead gallery. Pointer indicates where mine started. Current feeding area has not yet healed.over. Photo by JHH (9776A)

Figure 8

Melanophila galleries of 1936 brood, as of September 1, 1936, showing where galleries first affected wood, where healing occurred, and where the then current feeding was taking place. Two larvae are shown in place. Photo by KAS (9749)

Figure 9a

Showing larval mine effect in phloem ending in pitch pocket in which larva is imbedded. Photo by KAS (9744A)

Figure 9b

Counterpart of 9a showing healed over gallery in wood and 1936 growth starting to cover pitch area. Photo by KAS (9744B)

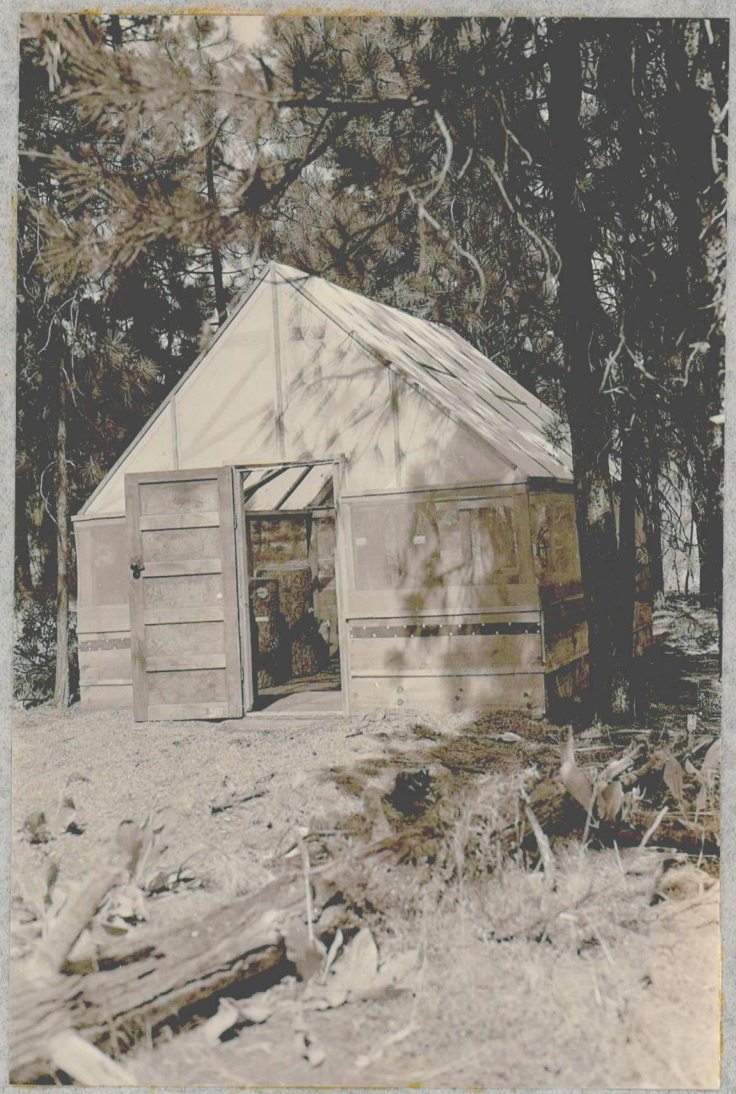


Figure 10

12' x 14' insectary at Hackamore Field Laboratory. Galvanized screening on sides and heavy cheesecloth on roof. Paraffined legs visible standing on floor. Photo by KAB (9748)